

# RECENT TRENDS IN PLANT PHYSIOLOGY<sup>1</sup>

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It is a privilege to be the first to have the floor in this "Forestry Physiology Symposium," and I wish to start by paying a brief tribute to the background of circumstances which has prompted this occasion. This year marks the 75th anniversary of the establishment of the Ohio Agricultural Experiment Station and this symposium represents one of the special events which has been planned in recognition of this fact. It seems especially fitting that a program in forestry should be one feature of this anniversary year, since forestry has long occupied a prominent place in the program of the Ohio Agricultural Experiment Station. The Secrest Arboretum, to mention only one aspect of the forestry program, is now, and long has been, a distinctive and valuable feature of this institution.

The topic on which I have been asked to speak is that of "Recent Trends in Plant Physiology." I presume that the objective of my remarks should be to provide a generalized backdrop of ideas for the presumably meatier intellectual fare which is to follow. In one way this is an easy topic to speak on; its very breadth gives me plenty of leeway. In another way it is a very difficult topic, because the problem of setting its boundaries is left completely in my hands. For example, what construction shall I put on the word "recent"? This is an elastic word but I am not going to stretch it too far; the pertinence of my remarks will extend backwards in time for not more than ten, or at the most, fifteen years.

I propose to discuss this topic under four main categories: (1) trends in points of view, (2) trends in research emphasis, (3) trends in experimental techniques, and (4) trends in the kinds of plants used for experimentation.

The most pronounced change in the approach to many phases of plant physiology in recent years has been the shift from a chemical to a biochemical viewpoint. Even the chemical approach to plant physiology, in any comprehensive sense of the word, does not date back much further than the beginning of the present century. Prior to that time much emphasis was placed on the so-called stimulus-response physiology, with no very serious attempts to probe internally into the accompanying processes.

Toward the close of the Nineteenth Century, chemistry first began to achieve real stature as a science. Under the impact of a wave of important discoveries, supported by brilliant theoretical interpretations, by such men as Arrhenius, van Hoff, Perkin, Gibbs, Ostwald, Raoult, Freundlich, and Kekulé, chemistry became the most respected of all sciences. At this period all of these stars, and many others, shone so brilliantly in the chemical heavens that all of science was illuminated. The new era in physics was not to dawn for another quarter of a century.

The many significant advances made in chemistry during the late Nineteenth and early Twentieth centuries led to a marked increase in attempts to interpret physiological processes in terms of chemical principles. Many plant processes were investigated and interpreted from this viewpoint, but one example will suffice for the present discussion. The well known formaldehyde theory of photosynthesis, first suggested by Baeyer in 1870, was still being supported by investigators of note as late as the early thirties. Anyone who is even casually familiar with current literature on the mechanism of photosynthesis realizes how widely

<sup>1</sup>Papers from the Department of Botany and Plant Pathology, The Ohio State University, No. 612.

the long respectable formaldehyde theory fell wide of the mark, yet from the purely chemical viewpoint, it was a perfectly valid and plausible hypothesis. Not all interpretations of plant physiological processes from the viewpoint of chemistry during this period proved as inadequate as the example given. By and large, however, the results of probing into the nature of physiological mechanisms from this viewpoint did not prove as fruitful as many investigators of that period had hoped.

Although there is a very real difference between the two, it is difficult to put into exact words the distinction between a chemical and a biochemical viewpoint. The former might be described as that of test tube chemistry. But the reactions of living organisms do not occur in test tubes. Neither can they be wholly explained by the principles of test tube chemistry. In biochemistry reactions a straight line is not necessarily the shortest distance between two points. From the viewpoint of the conventionally-minded chemist, the reactions which occur in living organisms appear devious and circumlocutory. This does not mean, of course, that the recognized principles of chemistry have been repealed in the biochemical world. Rather it means that these same principles are at work in systems which rarely, if ever, exist outside of living organisms, and it is this different framework of operation which gives to biochemical reactions their distinctive aspects.

One example may serve to illustrate and clarify the immediately foregoing remarks. The late William Lloyd Evans, longtime and well-known professor of chemistry at The Ohio State University, was a recognized authority on carbohydrate chemistry about a generation ago. Among other carbohydrate problems which he studied was that of their stepwise degradation under various conditions. Dr. Evans succeeded in working out the sequences of reactions involved in such breakdowns of carbohydrates in great detail. But it was noteworthy that, in the inanimate systems with which he was dealing, such degradative reactions only occurred in the presence of a strong acid, or a strong alkali, and that high temperatures were also often required. I remember discussing with Dr. Evans on several occasions what possible light his findings could throw on the degradation of carbohydrates in living cells. The problem was not illuminated by his work because strong acids, strong alkalis, or high temperatures do not exist in living cells.

Actually, as of today, not much more than twenty-five years later, the stepwise degradation of the carbohydrates is one of the most thoroughly understood aspects of cellular metabolism. The process as it occurs in living cells does not remotely resemble what went on in Dr. Evans' test tubes. It has been investigated in mammalian tissues, in microorganisms, and in the tissues of higher plants, and seems to be basically similar in all kinds of living cells. Even the beginnings of progress in elucidating this complex phenomenon were not made, however, until it was studied in relation to the compounds and systems actually present in living cells. Only in terms of enzymes and coenzymes, hydrogen acceptors and donors, phosphate acceptors and donors, and low and high energy bonds could this complex process be resolved into its component reactions. Counterparts to all these entities also exist in nonliving systems but seldom if ever in such complex arrays as they are found in living cells.

Let us now turn our attention to recent trends in research emphasis in the realm of plant physiology. Preeminent among these is the field of plant metabolism by which is meant all of the reactions and chains of reactions, forwards, backwards, sidewise and cyclical, occurring within the metabolic pool in the matrix of the protoplasm. More than in any other field advances in this phase of physiology have been dependent upon a biochemical foundation and the adoption of a biochemical viewpoint.

In recent years our knowledge of the metabolic pool in plants, with its numerous eddies, cross currents and whirlpools, has steadily become wider and deeper.

The metabolic pathways in the oxidation of carbohydrates, as previously indicated, are quite well understood. The biochemistry of photosynthesis, although not, parenthetically, its energetics, is approaching a comparable status of knowledge. Similarly, knowledge of the metabolism of organic acids, fats, and nitrogenous compounds has progressed substantially in the last decade or two. The general advance in our understanding of the overall dynamics of plant metabolism has been one of the most outstanding achievements of plant physiology during the last two decades.

Research in plant hormones is another field of investigational activity which has retained its prominence in recent years. Work on the auxins has continued at a steady pace and substantial progress has been made in understanding many of their properties except the most basic one of just what is their metabolic role in the plant cell. Plausible concepts have been worked out relating the structure of molecules to their effectiveness as auxins. The kinetics of auxin action have been studied and not unsurprisingly have been found to resemble the kinetics of enzymatic reactions. Rational explanations for the action of antiauxins in counteracting effects of auxins have been developed on the basis of a mechanism of competitive inhibition.

Work on other kinds of plant hormones besides the auxins has continued in recent years, and some entirely new ones have been discovered. Investigations have continued on the roles of thiamin, niacin, pyridoxine and other plant hormones of the B vitamin group. Probably much more epoch-making in its implications, however, is the recent discovery by a team of research workers at the University of Wisconsin of the cell-division promoting hormone called kinetin. The roles of this hormone and the probably other similar compounds in plants are still largely unexplored, but it seems likely that hormones of this type may be found to rank with the auxins in the universality of their effects.

And finally we must not overlook the latest cinderella of plant hormones, gibberellic acid. Although studies of this substance have scarcely advanced beyond the "spray it on and see what happens" stage, its introduction has been accompanied by such a flux of publicity that almost everyone has heard of it. There are more articles about gibberellic acid in popular journals than in scientific ones. Sometimes known as the "neck-stretching" hormone, because its most spectacular effect on plants is to promote the elongation of stems and other organs, gibberellic acid has also been reported to have many other effects on plants. Among these are the induction of flowering in certain species under conditions which otherwise do not induce flowering. Practically all work on this hormone to date has been of a preliminary nature and a true appraisal of its role in plant growth and metabolism must await further experimentation. Likewise, such practical applications as this substance may ultimately prove to have must await a better understanding of its basic physiological effects.

In the above paragraphs I have discussed hormones only in the narrower sense of compounds known to be endogenous synthetic products of plants. As is well known, many compounds not known to be natural plant metabolites have hormonelike effects on plants. Two-4 dichlorophenoxyacetic acid (2,4,D) and maleic hydrazide, to mention only two of the better known ones, are examples of compounds in this category. Most experiments on effects of nonendogenous hormones on plants have been empirical in approach and, in my judgment, will therefore not yield scientific profits of lasting benefit, either in their basic or applied aspects. A deeper insight into the roles played by such compounds in plant metabolism will give a sounder basis for judging their possible uses from more practical standpoints.

One other strong research trend in recent years which deserves mention has been an expanded interest in the photoreactions of plants. Although such long-favored lines of research as the action spectrum of photosynthesis and the quantum

efficiency of photosynthesis have not been entirely neglected, much of the work on photoreactions in recent years had its genesis in investigations on photoperiodism. Pioneer investigations on the action spectrum of the low energy light reaction of photoperiodism and certain other light-sensitive processes by Borthwick, Parker, Hendricks and their associates at Beltsville, Maryland, led to the discovery of the reversible red  $\rightleftharpoons$  far-red reaction in the physiology of plants.

The essence of this finding is that in various light-sensitive reactions a narrow band of wave lengths in the red with a peak at about 6600Å causes the reaction to go in one direction, while an adjacent band in the far-red with a peak at about 7350Å causes the same reaction to go in the opposite direction. In general, also, the reaction goes the same direction in the dark as under far-red irradiation, but at a much slower rate. Furthermore the reaction is reversible, often for an indefinite number of times. In light-sensitive lettuce seed for example, brief exposure of the seed to the red band of light greatly promotes its germination. If the exposure to the red band is followed shortly by a brief exposure to the far-red band, the promoting effect of the red light is mostly or entirely offset. A second exposure to red following the exposure to far-red has a promoting effect on germination, while a second exposure to far-red following the second exposure to red has an inhibiting effect. The reversibility of the reaction has been demonstrated to extend over a long series of alternations between irradiation with red and with far-red light.

The most amazing feature of this reversible reaction is the multiplicity of plant physiological phenomena and processes in which it appears to play a role. Among these are the photoperiodic reactions of both long and short day plants, the germination of light sensitive seeds, the elongation of coleoptiles, hypocotyls, and epicotyls, the expansion of leaf blades, the germination of fern spores, and the synthesis of flavone pigments. Other phenomena in which it is believed, although not as yet experimentally confirmed, that this distinctive light reaction may also play a role are anthocyanin formation, succulency, tillering, epinasty, bulb formation, tuberization, abscission, fasciation, cambial activity, and sexual expression.

The array of dissimilar processes in which this reaction appears to play a role is one of the most fascinating discoveries in all of botanical science in recent years. Unquestionably one of the master or key reactions in plant metabolism has been revealed by investigations in this field of photophysiology. In this respect this reversible photoreaction resembles the reaction catalyzed by auxin which is also obviously a key reaction in plants.

Let us now turn our attention to recent trends in the kinds of experimental techniques being used. I will mention first the employment of artificially controlled environments for physiological investigations with plants. Such artificially controlled environments usually take the form of small rooms in which at least the factors of light and temperature are controlled, and often others as well. Although earlier attempts to construct such facilities had been made, and temperature and humidity controlled dark rooms for auxin work date back about a quarter of a century, it was not until the advent of modern refrigeration engineering and of the fluorescent lamp that the development of such research facilities for plant physiological research became generally feasible. Ten years ago such controlled environment rooms were a rarity; today there is scarcely an institution pretending to do serious research on the physiology of plants which does not possess one or more.

Pioneer work on the development of such rooms was done by Parker and Borthwick of the U. S. Dept. of Agriculture and their light room at Beltsville was one of the first effective installations of its kind.

The most outstanding and well-known example of an installation for the growing of plants under controlled environments is the Earhart Plant Research Laboratory which was developed under the direction of Dr. Frits Went at the California Institute of Technology. This unique installation, often called the

"phytotron," comprises fifty-four separate units, many of which are air-conditioned greenhouses and darkrooms. There are thirteen rooms in which the factors of temperature, humidity, and light are all artificially controlled. In certain rooms still other factors such as wind velocity, rainfall, fog, and composition of the atmosphere are also controlled. The ionic environment of the roots and other substratum conditions are kept under control by growing all plants in gravel irrigated by suitable culture solutions. Special precautions are also taken to maintain, as nearly as possible, sterile conditions throughout the phytotron. Since Pasadena has been engulfed by the smog belt, it is probable that the only really healthy plants in town are those growing in the filtered air of the phytotron!

It should perhaps be emphasized that controlled conditions—at least in biological work—do not usually refer to constant conditions. Temperature and light, clearly the most significant of the environmental factors from the standpoint of most physiological processes, represent the irreducible minimum of factors which must be controlled if results of any significance are to be obtained. Temperature control is usually so arranged that dark period temperatures are lower than light period temperatures. Light is controlled with respect to length of the photoperiod, and, within limits, at least, in irradiance and quality. For many important types of physiological work with plants, control of no more than these two factors is adequate.

The obvious advantage of controlled climate rooms is that of reproducibility of experimental conditions from one experiment to the next. A group of plants can be exposed to the same environmental conditions in July, for example, as another group raised in January. Or, what is perhaps even more important, experiments conducted in one laboratory can be exactly duplicated in another laboratory. Furthermore, systematic variation of environmental factors from one experiment to the next can be accomplished in no other satisfactory manner than by the use of suitably equipped climate control rooms. Operation of a number of such rooms simultaneously obviously provides the most flexible facilities for such experimentation. Even when only one environment control room is available, however, such experiments can be performed, if the range of operation of that room is sufficiently flexible, by running the experiments in series.

The wide use in recent years of environment control rooms has led to immeasurable progress in increasing the accuracy of our knowledge of various growth reactions of many species of plants, especially to the factors of light and temperature. The almost spectacular advances in our knowledge of photoperiodism in plants in the last decade would scarcely have been possible without the employment of such facilities. Likewise knowledge of temperature effects on plants has been greatly advanced by such facilities.

A second widely used and potent new technique of physiological research has been made possible only by the advent of the modern alchemist who operates in the realm of physics rather than of chemistry. By unleashing powers only dreamed of yesterday he can, in the cyclotron and nuclear reactor, bring about the transmutation of one kind of atom into one of its isotopes, or even into an atom of an entirely different species. Many of these artificially produced isotopes are radioactive. That certain naturally occurring atoms such as radium, thorium, and uranium are radioactive has long been known, but it has been only for a comparatively few years that it has been possible to endow many of the physiologically important elements with the property of radioactivity. Some of the radioisotopes which have been most widely used in plant physiological research are  $\text{Na}^{24}$ ,  $\text{P}^{32}$ ,  $\text{K}^{42}$ ,  $\text{C}^{11}$ ,  $\text{C}^{14}$ ,  $\text{S}^{35}$ , and  $\text{Ca}^{45}$ .

Such radioisotopes constantly betray their presence, wherever they may be, by the continuous emission of radiations or charged particles which can be detected by suitable instruments. If such radioisotopes are incorporated into molecules, it is often possible to trace their pathway through an organism, after absorption

or ingestion, and even to discover the chemical reactions in which they participate. This has never been possible by conventional methods of chemical analysis because by such methods it is impossible to distinguish between the introduced molecules and other molecules of the same species which were already present in the organism.

Some stable isotopes, of a mass unlike that of the most common isotope of the same element, have also been used as tracers in the investigations of various plant processes. The presence of such non-radioactive isotopes can be detected with a mass spectrograph. Several such isotopes which have been widely used in plant physiological research are  $H^2$ ,  $O^{18}$ ,  $C^{13}$ , and  $N^{15}$ .

So extensively have stable and radioactive isotopes been used in the investigation of plant physiological problems that it is difficult to realize that these techniques have been available for less than 20 years. Isotopes have been used as tracers especially in following the route of translocation of various kinds of solutes through plants and in the investigation of metabolic pathways.

The first critical demonstration that the upward movement of mineral salts absorbed from the soil occurred through the xylem of plants was made by the use of radioisotopes by Stout and Hoagland in 1939. Downward translocation routes have also been followed in similar fashion by introducing radioactive compounds into leaves, and many other aspects of the absorption and translocation of solutes are amenable to experimentation in which isotopes are employed as tracers.

The metabolic pathways in photosynthesis, respiration, amino acid synthesis and other similar processes have been explored extensively by isotope tracer techniques. When leaves, or algae, for example, are allowed to absorb carbon dioxide in which the carbon is isotopically distinctive, and the reaction stopped by killing samples of the tissue at various intervals after the start of the experiment, important clues as to the metabolic sequence of events can be obtained. The kinds of compounds into which the labelled carbon has been incorporated after different time intervals can often be ascertained. Chromatographic techniques, to which further reference will be made later, are often used in order to separate and identify the compounds into which the isotopically distinctive carbon has been incorporated. By a similar technique, the source of the oxygen liberated in photosynthesis has been shown to be largely, if not entirely, from the water molecules, rather than from the carbon dioxide molecules. By using alternatively water and carbon dioxide made with the  $O^{18}$  isotope of oxygen as raw materials in photosynthesis, it has been possible to make a decision regarding this basic fact in the mechanism of photosynthesis.

Although, strictly speaking, more of a biochemical than a physiological tool, no account of recent trends in techniques would be complete without some mention of paper chromatography. The use of this method is generally considered to have started with the work of Cosden, Gordon and Martin in 1944. Although other factors are also involved, the basic principle of paper chromatography is that of the partition of a solute between two immiscible liquid phases. The method is a micro one, as only very small quantities of test solution are used. It can be employed for the separation and subsequent identification of a number of the components in solution in a single sample.

A variety of paper chromatographic techniques have been developed, one of the most widely used of which is two-dimensional chromatography. The essentials of this method can be described in a few sentences. A piece of suitable filter paper is cut to suitable dimensions, a square piece 50 cm. on an edge being a representative size. A small drop of the test solution is applied near one corner of the paper and allowed to dry. Sometimes, in order to introduce a larger sample into the system, several drops are applied, each being allowed to dry before the next one is added. The paper is then suspended with its lower edge in the first liquid to be used until it has risen by capillarity almost to the top of the sheet.

The sheet is then dried, and resuspended in a second liquid whose front is at right angles to that of the first liquid. The first liquid used might, for example, be water-saturated phenol, the second  $\alpha$ -picoline-water, but many other combinations are employed.

As a result of this procedure, for reasons too complex to enter into in this brief review, the various components of the sample become distributed on the paper according to a definite pattern, each, however, usually being restricted to a relatively small area. After such a separation has been achieved the position of the various spots on the chromatogram can be detected by various procedures, such as by color reactions, by autoradiography (for tagged compounds), by fluorescence or absorption in the ultraviolet range, or by microbiological reactions. The location of the spot in itself serves to identify or help identify the compound which it represents, but this can be followed by confirmatory qualitative tests, and often also by quantitative tests for the substance concentrated in any given area of the chromatogram.

The technique of paper chromatography has been applied to the micro-separation and microanalysis of virtually every known class of chemical compound from inorganic ions to some of the most complex known organic compounds. Its applications to problems in the biological sciences are legion. In the realm of plant physiology, for example, it has been used for the separation and identification of the intermediates of photosynthesis and other metabolic processes, for the identification of the individual amino acids occurring in plant tissues of various kinds, and for the separation of auxin and auxinlike compounds extracted from plant tissues.

I shall now speak briefly on trends in the kinds of plants used in experimentation. Algae have come increasingly into prominence as experimental organisms in recent years. *Chlorella*, first used as an experimental plant in photosynthetic work by Warburg nearly 40 years ago, is still a favorite. Several species and various strains of this alga have been employed. Other species of green algae such as *Chroococcus* and *Scenedesmus* have been used in various kinds of physiological work as have also a number of species of the blue green algae such as *Anabaena*, *Nostoc*, *Calothrix*, *Coccochloris*, *Periocyctis* and *Diplocystis*. Recent work on the blue green algae has been stimulated by an increasing realization of the role of this group of organisms in nitrogen fixation.

Several reasons can be advanced for the increasing popularity of algae as laboratory test organisms. Many of them can be obtained in pure culture which is a definite advantage for certain types of research. Two universities in this country, Indiana University and the University of Georgia, have recently developed stock collections of hundreds of species and varieties of algae, mostly in pure cultures, from which subcultures can be obtained by interested investigators for physiological or other types of research. Such stock culture collections of bacteria and fungi have long been in existence, but establishment of such collections of algal cultures is, for this country, an innovation, although Cambridge University in England has long possessed one.

The obvious convenience of working with small samples which nevertheless represent thousands of individual organisms has endeared the algae to many investigators, especially those working on such fundamental problems as the mechanism of photosynthesis. The use of algae as the test organisms in such researches has continued in recent years with little abatement.

Another source of impetus to study of the physiology of algae is the prospect that mass culture techniques may be developed to a degree of practicality that will permit raising of algae as a supplementary source of food or raw materials. There is no doubt that such procedures are technically feasible; the major consideration yet to be resolved is whether or not they can also be made economically feasible. Substantial recognition of this possibility was made at the recent World

Symposium on Applied Solar Energy held in Tucson and Phoenix, Arizona, at which four full half day sessions were devoted to the green plant as a solar energy converter. By far the larger part of this time was devoted to the algae, and the possibility of mass culture of algae on a commercial basis received substantial consideration in the deliberations.

Fungus physiology is another branch of plant physiology which has received increasing emphasis over the past decade or two. Less than a generation ago only one botany department in this country offered a course in the physiology of the fungi; today practically every major botany department in the country lists such a course among its offerings. A major source of impetus to increased interest in fungus physiology has been the discovery that certain species of fungi are important sources of antibiotics. The discovery of penicillin and the subsequent development of its production on a commercial scale is a story which is well-known to every enlightened citizen.

Although fungi lack the fundamental solar energy conversion feature of metabolism which is the basic process of chlorophyllous plants, nevertheless their metabolisms are often so distinctive as to result in the synthesis of compounds which are useful to man. By proper selection of species and varieties, by development of the most suitable cultural conditions, and by the use of large scale industrial production techniques, certain so-called fermentation processes of fungi have been used for the commercial production of various useful compounds. The best known of these are ethyl alcohol and citric acid.

Latterly, wide use has been made in a practical way of the propensity of certain fungi to synthesize, as previously mentioned, certain complex compounds which act in an antibiotic capacity. Among the better known of these are streptomycin, terramycin, and aureomycin, all of which are synthesized by fungi of the actinomycetes group. Gibberellic acid, previously mentioned, is the latest addition to the biologically significant compounds being used by man which is a synthetic product of a fungus.

Passing on to a brief consideration of the vascular plants, two main trends seem to be at work in the kinds of plants used in physiological experimentation. Although by no means a new tendency, increasingly certain investigators and groups of investigators have specialized in the physiology of one plant, usually a species of economic importance. Thus, we see emerging substantial bodies of knowledge regarding the physiology of the corn plant, the physiology of the cotton plant, the physiology of the tobacco plant, and so forth. It is hoped that eventually investigations channelled along such lines will bear fruit in the form of monographs dealing with the physiology of such individual species. This is a desirable approach since the physiological requirements and behavior of no two kinds of plants are identical; indeed even different varieties of the same species often differ appreciably in their physiology. A thorough knowledge of the basic physiology of each economic species of plant is one of the primary requisites for enlightened cultural practices. We should know about the mineral nutrition, photoperiodic behavior, temperature relations, drought resistance, cold resistance, seed viability, dormancy of various organs, pollen viability, water requirement, light saturation for photosynthesis, and many other physiological characteristics of each such species. Much remains to be done along these lines.

Another increasing trend among workers with vascular plants has been that of intensive investigations of physiological phenomena in certain "guinea pig" species of plants. One advantage which the general plant physiologist enjoys as compared with the "one species" plant physiologist is that of choice in selection of his experimental plants. Some kinds of plants are intrinsically better adapted to certain kinds of physiological experimentation than others.

One well-known example of this trend is the extensive use of the oat coleoptile as the test object in biological assays of auxins. When oat coleoptiles are allowed



to develop for a limited time in the dark under certain conditions of temperature and humidity and especially if decapitated, the quantity of endogenous auxin present becomes very low, making such coleoptiles extremely sensitive to auxins from an external source. Within limits the growth or curvature of such coleoptiles can be used as a quantitative index of the amount of auxin with which it is brought into contact. A further advantage of oat coleoptiles as test objects is that large quantities of them can be raised in a small space, permitting many replications of a given test to be made with relative ease.

A similar example is the extensive use of the cocklebur as a test plant in photoperiodism experiments. In fact this is the only known use of cockleburs to the human race! This common weed species is distinctive in that only one short day photoperiodic cycle is sufficient to induce initiation of flower primordia in plants which are otherwise kept under long day conditions. To the best of my knowledge there is only one other species of which this is known to be true. In ways which any specialist on photoperiodism will recognize, the extreme photoperiodic sensitivity of this species has made it an uncommonly useful test plant in many studies of this phenomenon.

More practical minded plant scientists sometimes comment in a dubious or even sarcastic vein on what seems to them, the often unrealistic or even bizarre selections of experimental plants made by physiologists working on basic problems in the field. There is a commonly quoted statement, which originated, I believe, in the medical field, to the effect that "normal physiology is often revealed only by pathological conditions." There is a sound element of truth in this statement, but I do not believe it is a broad enough generalization. Behavior as revealed by species which are genetically unusual often helps in understanding reactions of other species in which the existence of certain reactions is less marked. Likewise, insight into physiological reactions or behavior under usual or normal patterns of environmental conditions are often revealed by subjection of plants to unusual or abnormal conditions. Reactions which are not otherwise apparent are often brought to light in this manner.

Since this is a symposium on forest physiology, I would like to be able to add that there has been a strong trend toward increased work on forest trees by plant physiologists in recent years. I believe there is a trend in that direction but cannot honestly say that it seems to be a pronounced one. The average plant physiologist looks at a full-grown tree, shakes his head, and turns his research endeavors in other directions, to work with *Chlorella*, perhaps, or maybe with bean plants. A tree is not a good laboratory plant for the same reasons that an elephant is not a good laboratory animal.

Actually, of course, the foregoing remarks are not a wholly accurate appraisal of the situation. While it is seldom possible to subject large, mature trees to laboratory or greenhouse experimentation, wide horizons are open for physiological research with tree seeds, cuttings, seedlings and small trees. And work with large trees is not precluded either although for such investigations the laboratory must go to the tree, rather than the tree go to the laboratory.

There are indications that we are on the threshold of a revitalized interest in tree physiology. This symposium is one evidence of such an increase in interest. Similar symposia held at Petersham, Massachusetts just recently and at Ottawa, Canada about two years ago are further such evidence. And just this past year there has been published a "Tree Physiology Bibliography," compiled by Dr. Theodore T. Kozlowski of the University of Massachusetts in cooperation with the U. S. Forest Service. About 4000 titles are listed in this bibliography. I do not believe it is any secret that Dr. Kozlowski, in co-authorship with Dr. Paul J. Kramer of Duke University, now has in an advanced stage of preparation the manuscript for a book on tree physiology. This will be a welcome addition to the literature, since such books and monographs as have been published in this general field of knowledge are long outdated.

And, in conclusion, I wish to say a few words about not what is a trend, but perhaps should be one. More than once I have heard this statement: "A botanist is a kind of a scientist who usually starts out with a living plant and most commonly ends up with a dead one." This is an indictment which cannot be too easily shrugged off. Consider the taxonomist who collects live plants and dries them into extinction; consider the morphologist who collects live plants and pickles them into extinction; consider the physiologist who collects live plants and grinds them into extinction. Although the above statement is admittedly a somewhat exaggerated one, there is nevertheless a valid element of irony in it. Botany is a life science, yet we work too much of the time with corpses, and sometimes unrecognizable corpses at that. Some of this is unavoidable, but let's keep as much life in our plants as possible. We need to put more emphasis on techniques which the plants can survive as living entities. We have some such techniques, but perhaps not enough. Perhaps one possibility would be a more extensive adoption of the biopsy techniques used by our colleagues in the medical sciences.

The great miracle of life is that it has evolved into and persisted in a thermodynamically inhospitable world. We owe a respect, and perhaps even a reverence, for this achievement by even the least human of living organisms. We should never forget that, as plant scientists, we are dealing with a basic and significant manifestation of life. I quote from the incomparable Emily Dickinson, who with the poet's true intuition, saw the same matter in a slightly different, but pertinent, context:

"Surgeons must be very careful  
When they take the knife!  
Underneath their fine incisions  
Stirs the culprit—Life!"

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